
COMPARISON OF THE RESOLVING POWER OF METRIC AND NON-METRIC CRANIAL CHARACTERS IN DEFINING GEOGRAPHICAL POPULATIONS OF DOLPHINS

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ABSTRACT. Resolving power was compared by multivariate analysis of 31 metric and 26 non-metric characters for three geographical samples of skulls of the common dolphin, *Delphinus delphis*: eastern tropical Pacific (73 specimens), western and mid-North Atlantic (71), and Black Sea (37). The samples from the three areas differed significantly in both the metric and the non-metric characters. The metric characters had higher discriminating power (97.8% correct classification by jackknife method) than the non-metric characters (82.5%), but both were efficient. The results of an analysis of combined metric and non-metric data are consistent with an hypothesis of non-neutrality of the non-metric characters. Because of their apparent lesser resolving power and because of difficulties concerning repeatability, it is recommended that non-metric characters be used in dolphin population studies only in combination with metric characters and that special attention be paid to controlling conditions to maximize comparability of data sets.

СРАВНЕНИЕ ПО РАЗРЕШАЮЩЕЙ СПОСОБНОСТИ МЕТРИЧЕСКИХ И НЕМЕТРИЧЕСКИХ ПРИЗНАКОВ ЧЕРЕПА ПРИ РАЗДЕЛЕНИИ ГЕОГРАФИЧЕСКИХ ПОПУЛЯЦИЙ ДЕЛЬФИНОВ

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Сравнение по разрешающей способности метрических и неметрических признаков было произведено при многомерном анализе 31 метрического и 26 неметрических признаков черепа обыкновенного дельфина, *Delphinus delphis*. Три выборки были взяты в восточной тропической части Тихого океана (73 экземпляра), в северо-западной части Атлантического океана (71 экз.) и в Черном море (37 экз.). Выборки из этих трех районов значимо различались как по метрическим, так и по неметрическим признакам. Метрические признаки обладали большей разрешающей способностью (97,8% правильных определений популяционной принадлежности особей при использовании метода складного ножа), чем неметрические (82,5% правильных определений), но и те, и другие эффективны. Результаты анализа объединенных данных по метрическим и неметрическим признакам согласуются с гипотезой, в соответствии с которой неметрические признаки не нейтральны. Поскольку неметрические признаки обладают меньшей разрешающей способностью и поскольку при получении воспроизводимых оценок этих признаков возникают трудности, рекомендуется их использовать при исследовании популяций дельфинов только в сочетании с метрическими признаками, уделяя особое внимание соблюдению условий, обеспечивающих максимальную сопоставимость данных.

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INTRODUCTION

Non-metric characters (features coded by state, e.g., “present” or “absent”) are potentially more useful than metric characters for discriminating populations of mammals because (1) a large number of relatively independent characters can more easily be defined and (2) the characters are supposedly more “neutral” in relation to adaptation and therefore good indicators of degree of gene flow between populations (Sjøvold, 1973; Hartman, 1980). An additional attraction of non-metric characters for the cetologist is that they are less affected by preparation methods and specimen handling; for example, dolphin skulls in museums very frequently have broken rostra or dried tissue remaining on the rostrum tips, broken pterygoids, etc., and this often leads to missing values for several measurements.

Non-metric characters have been used in population analysis of several marine mammals: gray seals, *Halichoerus grypus* (Berry, 1969); ribbon seals, *Phoca fasciata*, and spotted seals, *P. largha* (Fedoseev, 1984); pantropical spotted dolphins, *Stenella attenuata*, and spinner dolphins, *S. longirostris* (Perrin et al., 1982; Yablokov et al., 1983); and harbor porpoises, *Phocoena phocoena* (Kinze, 1985, 1990), but the quality of their analytic power relative to that of metric characters has not been critically examined. The purpose of the present study was to compare the power of comparable suites of metric and non-metric characters to discriminate among manifestly isolated populations of dolphins—in this case, three geographically isolated populations of the short-beaked common dolphin, *Delphinus delphis*—with the intention of possibly using only one or the other of the two kinds of characters in future analyses of population structure for this and other dolphin species.

MATERIALS AND METHODS

THE SAMPLES

A total of 181 skulls of sexually mature adults was included in the analyses (Appendix 1). They came from the eastern tropical Pacific (73), the western and mid-North Atlantic (71), and the Black Sea (37). Distal fusion of the premaxillae and maxillae was used as an approximate criterion of sexual maturity (Dailey and Perrin, 1973). The eastern Pacific skulls (in the U.S. National Museum of Natural History [USNM], Washington, D.C.) were of dolphins killed incidentally during commercial tuna-seining operations. The dolphins were captured in nine purse-seine hauls by several vessels over a period of three weeks in the same general area in oceanic waters off Central America. The common dolphins in this area are thought to belong to a single breeding population (Perrin et al., 1985). The North Atlantic specimens (also in the USNM) came from standings and scientific captures and from incidental kills in commercial trawls and purse seines along the east coast of North America from Nova Scotia to Florida (67) and the mid-North Atlantic; it is not known how many breeding populations are represented in this sample. The Black Sea material (in the Zoological Museum of Moscow State University) came from the former Soviet commercial dolphin fishery; the population there

has been recognized as a subspecies, *Delphinus delphis ponticus* (Tomilin, 1957).

METRIC CHARACTERS

Twenty-seven skull measurements were taken as described in Perrin (1975) and are listed in Appendix 2. Tooth counts were treated as continuous variables, for a total of 31 metric variables.

NON-METRIC CHARACTERS

For the non-metric analyses, we began with the characters used in Perrin et al. (1982) and Yablokov et al. (1983). Analyses were performed before the final scorings to quantify variation among observers, variation with sex of the specimen, and correlations among the characters. Preliminary results of these analyses were reported in Perrin et al. (1988). Upon examination of *Delphinus* material at the Southwest Fisheries Science Center and a preliminary fist-round scoring of the eastern tropical Pacific series at the USNM by WFP and AVY (in 1987), we deleted some of the characters and added others, to arrive at a total of 62. A number of additional characters were considered but not included, because of very low variability or difficulty of scoring. WFP and AVY then each scored the series independently twice, with redefinition, deletion, and addition of characters between the rounds, to generate two separate data sets (WFP and AVY). Logistics prevented simultaneous “blind” scoring of all specimens at the same location and time.

Methods Used for Correlation Analyses

It is to be expected that at least some of the non-metric variables that were scored would be highly correlated with others. In such cases, it may be possible to drop one or more characters without losing significant information. When using metric variables, the Pearson product-moment correlation coefficient is typically used to describe such inter-relationship between variables. We used a non-metric analog to the Pearson statistic which calculates a coefficient of correlation based on a chi-square approach (Urbach, 1964). The coefficient, R , can have values ranging from 0 (no correlation) to 1.0 (perfect correlation). It is calculated as

$$R = \frac{\text{chi-square}}{\text{maximum possible chi-square}} \\ = \frac{\chi^2}{N\sqrt{(k_a - 1)(k_b - 1)}},$$

where N = number of specimens, k_a = number of classes of character A , and k_b = number of classes of character B .

The significance of the resulting correlation was determined by applying a chi-square contingency test. Correlation coefficients were therefore not calculated for some characters that had only two states with observations (a common state and a very rare state). For purposes of the analyses, the states of characters with more than three states (i.e., numbers of foramina or fenestrations) were aggregated into three pooled “states,” e.g., 1–3, 4–6, and 7–9 for one character. The same approach was used for analysis of correlations with sex of the specimen.

Comparison of Observers

Agreement between WFP and AVY in the first round of scoring ranged between 100% and 55–60% for the initial

62 characters (Fig. 1A). After detailed discussion of the individual characters, 17 were dropped from the series because of low agreement, low variability, or problems of character-state definition. Seven new characters were devised and added to the series, for a new total of 52. Agreement in the second round of scoring was better (Fig. 1B), but there was still very significant disagreement (more than 10%) for about one-third of the characters.

Correlations among the Characters

Five hundred fifty-four correlation analyses were possible (the number of observations for each state of the characters was five or greater) for the WFP data set and 583 for the AVY set; details are given in Perrin et al. (1988). The total numbers of significant correlations ($p < 0.05$) between variables were 44 (WFP) and 46 (AVY). The expected number of significant comparisons given 550–600 pairwise tests is approximately 28–30 by chance alone. However, 19 of the significant correlations were common to both sets of data. Six (WFP) and seven (AVY) of the significant correlations occurred with paired left/right characters for the same skull feature; of these five were present in both data sets. We concluded that correlations between the characters are significantly more common than would be expected by chance alone and that an appreciable amount of the redundancy in the variables could be eliminated by using only one of a left/right pair of characters.

Correlations with Sex of the Specimen

For the WFP data set, 34 analyses of correlation with sex were possible; for the AVY set, 36 were possible. Four characters were significantly correlated with sex in the WFP set and five in the AVY set ($p < 0.05$). Only one or two characters could be expected to be significantly correlated with sex by chance alone. Two characters were correlated with sex in both data sets; these were considered to be good candidates for characters to be avoided in comparisons of samples with different or unknown sex compositions.

Further Reduction of the Character Set

Based on the results of the comparisons of observers, 18 of the 52 characters were dropped from the set for comparison of the geographical samples. These were the characters for which observer agreement was less than 90% in the second comparison round (Fig. 1B). One of the characters deleted because of low repeatability was also significantly correlated with sex in both of the data sets. Because many of the Black Sea specimens were of unknown sex, the other character correlated with sex was also deleted. Of the five character pairs with significant within-pair correlation in both character sets, either one or both members of the pair were deleted for three pairs based on low observer agreement as described above. For the other two such character pairs, only the left-side member was retained. After all these deletions, 31 characters remained in the set for the geographical analyses (not 26, as stated in Perrin et al., 1988). A further modification was to assign three possible states for all characters that were not counts of foramina, with the third state being “intermediate,” “at the level of . . .,” or “uncertain,” as appropriate, to allow more homogeneous analysis and interpretation of the data.

Upon examination of the Black Sea series, 5 of the 31 characters proved to be unusable because of damage to the specimens (see Discussion). The remaining 26 char-

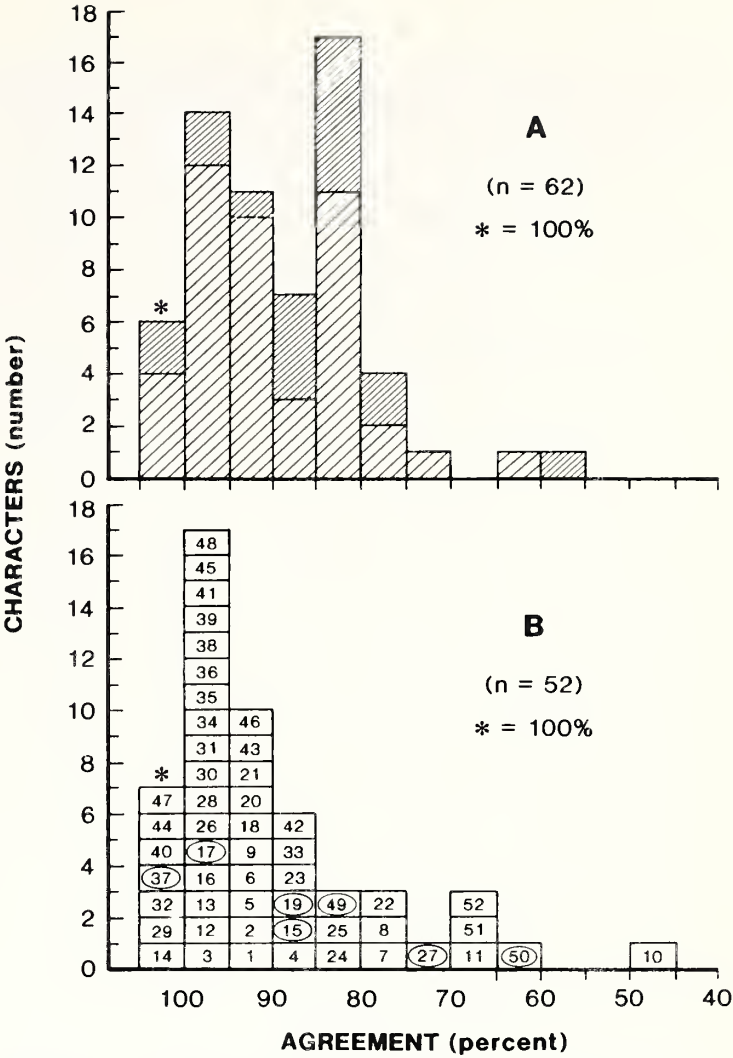


Figure 1. Histograms of percentage of agreement between WFP and AVY in (A) first round of scoring and (B) second round of scoring 73 skulls of *Delphinus delphis* for non-metric characters. In A, shaded portions represent characters deleted for the second round. In B, numbers represent characters as listed in Appendix 1 of Perrin et al. (1988); circled characters were added as new characters for the second round.

acters are described in Appendix 3. WFP and AVY measured and scored the Black Sea series in Moscow on 4–5 November 1988 and the two USNM series in Washington, D.C., from 31 March to 5 April 1989. For the non-metric characters, each scored all the skulls separately. The two sets of scores were compared, and differences were resolved through discussion and re-examination of the skulls, to arrive at a single agreed data set for each of the three geographical samples.

ANALYTICAL METHODS USED IN THE GEOGRAPHICAL COMPARISONS

The statistical analyses of both the metric and the non-metric data included two approaches. First, multivariate statistical tests were used to determine whether the measured traits were significantly different among the three geographical samples. Second, discriminant function analysis was used to determine how well collection location could be predicted from observed characters using a discriminant function which maximizes the difference among area samples.

Metric Analyses

A multivariate analysis of variance (MANOVA, BMDP4V, Dixon et al., 1990) was used to test whether the areas

Table 1. Statistics for skull measurements (mm) of geographical series of *Delphinus delphis*. Sample sizes in parentheses. See Appendix 2 for explanation of acronyms.

Measurement	Black Sea			Eastern tropical Pacific			Western North Atlantic		
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
1. CBLN	374–420 (36)	394.5	11.09	397–460 (73)	425.8	14.41	409–478 (68)	440.9	15.75
2. ROST	218–258 (36)	237.4	9.38	233–286 (72)	256.5	11.33	240–299 (69)	270.8	11.91
3. ROSW	75–87 (36)	80.9	2.87	82–103 (73)	92.3	4.37	81–102 (69)	89.9	4.54
4. ROSQ	49–59 (36)	53.8	2.57	51–68 (73)	60.5	3.43	53–70 (69)	61.9	3.53
5. ROSH	42–52 (36)	46.1	2.70	45–58 (73)	51.4	2.96	44–62 (69)	54.8	3.59
6. ROS3	29–42 (36)	33.9	2.66	33–44 (73)	38.3	2.40	32–47 (68)	40.0	3.79
7. PMXH	19–25 (36)	21.8	1.57	21–30 (73)	25.3	1.85	20–31 (69)	25.0	1.92
8. TIPN	264–305 (36)	283.2	9.64	281–339 (73)	307.8	13.11	279–345 (69)	317.0	14.30
9. TIPP	257–296 (23)	273.9	10.40	273–332 (72)	301.3	12.34	279–343 (67)	312.4	13.53
10. PREO	142–162 (37)	152.3	4.85	152–186 (73)	167.3	6.24	157–185 (69)	172.1	6.56
11. POST	164–182 (37)	172.7	4.67	173–203 (72)	187.2	6.45	177–204 (69)	191.5	6.49
12. ZYGO	161–179 (37)	170.6	4.44	171–200 (73)	184.3	6.41	173–202 (70)	189.1	6.71
13. EXTN	40–52 (37)	45.2	2.25	43–53 (73)	47.5	1.96	43–54 (70)	48.3	2.57
14. PMXM	62–75 (37)	67.8	2.64	68–82 (73)	74.2	2.74	64–84 (69)	75.2	3.75
15. PARI	128–150 (37)	140.1	4.86	139–165 (73)	152.1	5.09	143–165 (70)	153.7	5.09
16. BRNH	92–109 (37)	101.1	3.47	97–113 (73)	104.6	3.67	104–124 (70)	113.0	3.83
17. BRNL	100–114 (37)	107.4	3.58	105–124 (72)	115.1	3.67	110–132 (69)	119.9	4.24
18. FOSL	62–73 (37)	67.0	2.71	58–76 (73)	65.3	3.96	61–84 (70)	71.0	4.41
19. FOSH	45–57 (37)	50.8	3.02	38–60 (73)	48.3	3.94	48–64 (70)	55.2	3.46
20. ORBI	43–54 (37)	48.0	2.24	47–59 (73)	51.7	2.16	46–58 (69)	50.9	2.24
21. ANTO	34–45 (37)	38.8	2.61	38–53 (73)	43.9	2.70	39–54 (69)	47.2	3.22
22. INTN	46–54 (37)	49.5	2.45	47–59 (73)	52.6	2.71	45–65 (70)	56.0	3.69
23. UPRO	179–216 (34)	196.8	8.48	192–248 (73)	218.4	10.52	200–259 (69)	228.4	11.10
24. UPTL	41–48 (31)	44.7	1.97	43–54 (71)	49.0	2.47	42–53 (64)	48.3	2.26
25. UPTR	41–51 (33)	45.1	2.30	43–54 (72)	49.1	2.19	44–53 (64)	48.3	2.26
26. LOTL	43–51 (32)	46.3	2.02	43–54 (70)	47.9	2.50	44–52 (64)	47.1	2.11
27. LOTR	43–50 (32)	46.3	2.04	42–53 (71)	47.9	2.57	43–53 (64)	47.1	2.20
28. LORO	180–210 (33)	196.9	7.89	190–230 (72)	214.3	8.91	195–255 (67)	225.1	11.71
29. RAML	307–352 (33)	334.3	10.47	334–391 (72)	360.5	12.63	350–411 (67)	377.4	14.08
30. RAMH	59–67 (33)	61.6	1.92	59–70 (72)	64.2	2.26	62–75 (68)	68.5	2.88
31. TOOW	2.6–3.4 (29)	3.13	0.156	2.6–3.4 (64)	2.98	0.173	3.0–3.9 (47)	3.40	0.215

differed in the metric characters. Stepwise discriminant analysis (BMDP7M, Dixon et al., 1990) was used to identify metric characters contributing to the discrimination of source area. In this analysis, variables are entered one at a time, based on their ability to improve on the separation of the sample means (estimated as a linear combination of variables). Variables are added until the improvement of separation based on an F-ratio test falls below an arbitrary value (in this case, $F < 4.0$). (Note: We view this approach as empirical and do not ascribe statistical significance to variables that it identifies.) Jack-knife methods are used to estimate the number of cases (skulls) that are correctly identified; i.e., each specimen is classified based on a discriminant function that is computed excluding that specimen.

Three specimens (two from the North Atlantic and one from the Black Sea) were deleted from the metric analyses because of a large number of missing values, leaving a total sample of 178. Missing values for the remaining specimens were estimated using linear regression of the variable in question on the other variables (Dixon et al., 1990).

Non-Metric Analyses

Non-metric data violate many of the assumptions of standard multivariate tests designed for metric data. Therefore, we used an index of similarity Γ which tests pairwise group (in this case, area) differences in multivariate non-metric characters (Zhivotovskiy, 1982):

$$\Gamma_n = \sum_{i=1}^n \frac{r_i}{n},$$

where

$$r_i = \sqrt{p_1q_1} + \sqrt{p_2q_2} + \cdots + \sqrt{p_mq_m};$$

Γ_n = index of similarity for n characters; r_i = index of similarity for the i th character; $p_1, p_2, \dots, p_m$ = proportion of states 1, 2, . . . , m_i in one sample; $q_1, q_2, \dots, q_m$ = proportion in other sample; and m_i = number of states for character i .

The statistical significance of the above similarity index

Table 2. Statistics for stepwise discriminant analysis of skulls of *Delphinus delphis* from three areas based on metric characters.^a See Appendix 2 for explanation of acronyms.

Character	F-value to enter	Order of entry	Coefficients	
			I	II
16. BRNH	154.69	1	0.47163	0.02491
3. ROSW	82.90	2	0.56276	-0.26132
31. TOOW	29.13	3	-0.41130	0.20190
17. BRNL	21.80	4	-0.20619	-0.36730
15. PARI	14.39	5	0.55171	-0.47189
19. FOSH	28.90	6	-0.51689	0.39200
2. ROST	11.30	7	-2.08716	0.04097
8. TIPN	14.22	8	1.65711	0.59925
10. PREO	8.61	9	-0.28245	-0.48738
23. UPRO	7.47	10	0.36557	-0.80257
22. INTN	6.61	11	-0.28309	0.29144

a. For discriminant function; standardized by pooled within-group variances.

was tested using the method of Zhivotovskiy (1982). Given the following expression,

$$X = \frac{8N_1N_2}{(N_1+N_2)} \left(1 - \sum_{i=1}^n r_i - \frac{Z_0}{4} \right),$$

where N_i = number of individuals from group i and Z_0 = number of cases with zero observed frequency in one group but not in the other, it can be shown that X is distributed approximately as χ^2 with degrees of freedom equal to $\sum_{i=1}^n (m_i - 1)$ (Yablokov et al., 1983). This was tested using standard tables.

We also developed a simple bootstrap approach to test whether the non-metric traits differed among all areas simultaneously (analogous to an ANOVA test). The boot-

Table 4. Jackknife classifications for stepwise discriminant functions based on (a) 11 metric characters, (b) 8 non-metric characters, and (c) a combination of 7 metric and 2 non-metric characters. ETP = eastern tropical Pacific; WNA = western North Atlantic.

True group	Predicted group				Percent-age correct
	Black Sea	WNA	ETP	Total	
(a) Black Sea	36	0	0	36	100.0
WNA	0	67	2	69	97.1
ETP	1	1	71	73	97.3
Total	37	68	73	178	97.8
(b) Black Sea	28	0	9	37	75.7
WNA	4	61	4	69	88.4
ETP	9	5	57	71	80.3
Total	41	66	70	177	82.5
(c) Black Sea	36	0	0	36	100.0
WNA	3	62	2	67	92.5
ETP	3	2	66	71	93.0
Total	42	64	68	174	94.3

strap test statistic is based on the mean number of differences in character states for all pairwise specimen comparisons. The statistic used is the ratio, D , of the mean number of differences between groups to the mean within groups. Based on an assumption of no relationship between character states and area, the expected value of this ratio is 1.0. The expected distribution of the ratio given this null hypothesis was computed by Monte Carlo sampling. Group (area) membership was randomly assigned to each specimen (sampling without replacement and maintaining the observed sample sizes) and D was calculated. This bootstrap sampling procedure was repeated 1000 times and the probability distribution of D estimated. Statistical inference was based on a comparison

Table 3. Classification functions^a for stepwise discriminant analysis of skulls of *Delphinus delphis* from three areas based on metric characters. See Appendix 2 for explanation of acronyms. ETP = eastern tropical Pacific; WNA = western North Atlantic.

Character	Black Sea	ETP	WNA
2. ROST	1.62843	1.23656	2.17601
3. ROSW	0.01864	0.56331	-0.13070
8. TIPN	-0.35333	-0.29916	-0.92628
10. PREO	1.34214	1.59824	1.80625
15. PARI	2.07914	2.70658	2.13252
16. BRNH	3.26663	3.03982	3.66798
17. BRNL	4.32538	4.63624	4.87718
19. FOSH	0.60288	-0.16514	0.58942
22. INTN	-0.08477	-1.68253	-1.19496
23. UPRO	-0.71854	-0.30765	-0.50764
31. TOOW	54.83513	45.05722	57.18664
Constant	-793.27875	-890.32617	-983.51996

a. Used with original measurements. Add products of measurement and corresponding function values to constant; classify to area depending on which results in highest value for classification function.

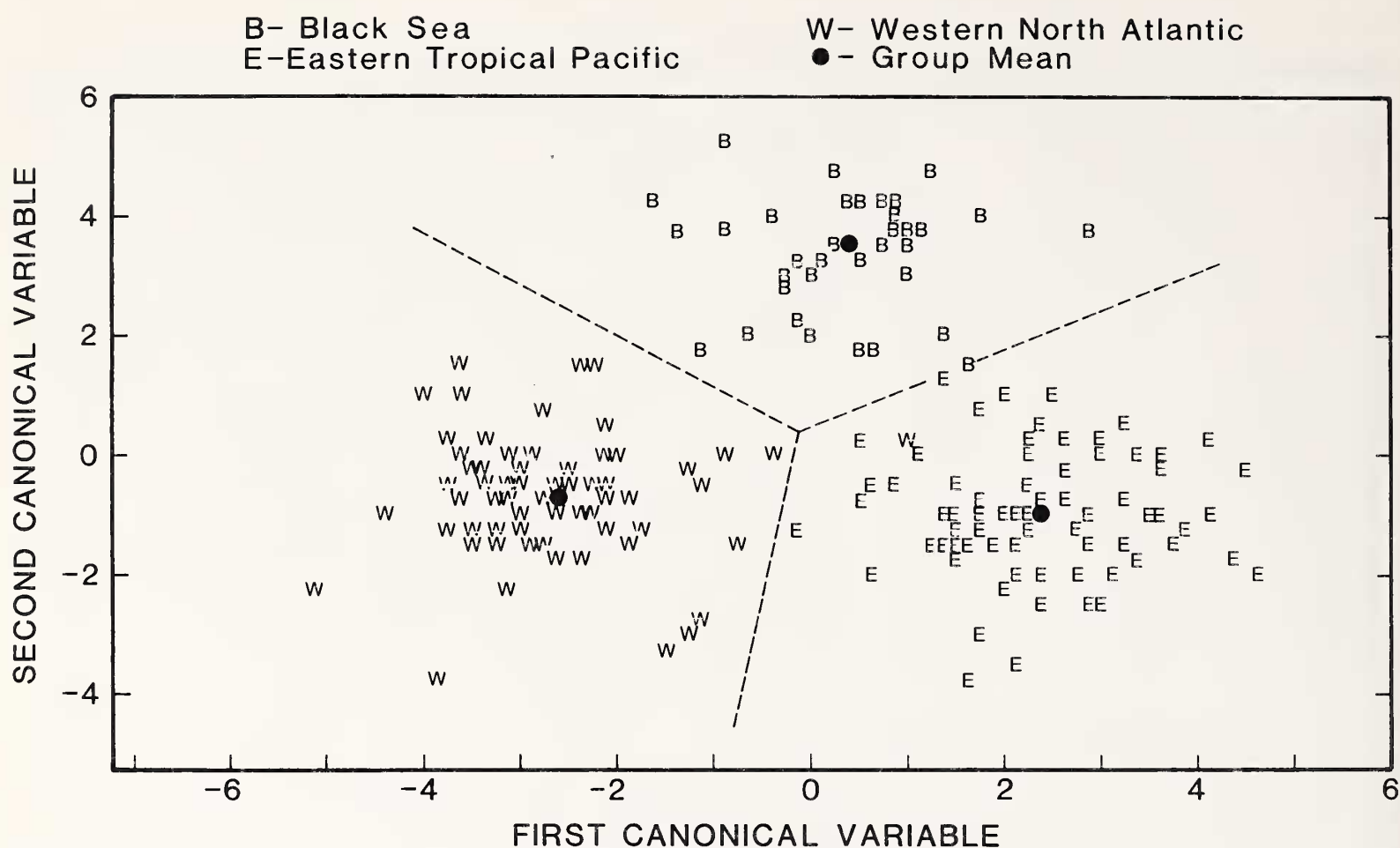


Figure 2. Results of discriminant analysis of geographical samples of skulls of *Delphinus delphis* based on metric characters.

of the observed value of D to its expected distribution given the hypothesis of no difference between areas.

A transformation of the non-metric data was required before they could be analyzed with standard discriminant analysis. Of the 26 non-metric characters, 21 had three observed states (coded 0, 1, or 2) and 5 characters had two observed states (coded 0 or 1). Because these coded values are arbitrary, they could not be used directly in a linear model such as discriminant analysis. The non-metric variables were therefore converted to binary variables. A character that can assume only one of two possible states was represented by one binary variable. A character that could assume one of three possible states was coded as two binary variables, with values 0/0, 0/1, and 1/0. The original 26 non-metric characters were thus converted into 47 binary variables. A stepwise discriminant analysis (BMDP7M, Dixon et al., 1990) was used to identify which binary (or dummy) variables added to the discrimination of area. (It is important to note that when a character is coded as two binary variables, only one of these might contribute to the discrimination.) As with the metric data, the F-ratio for inclusion was set at 4.0 and classification of specimens to area was evaluated with jackknifed classification.

Four specimens (two from the eastern Pacific and two from the Atlantic) were eliminated from the non-metric analyses because of missing values, yielding a total sample size of 177.

Combined Metric and Non-Metric Analyses

We also applied discriminant function analysis to a combination of metric and non-metric characters. Only those metric characters or non-metric binary variables which we found to contribute significantly to either the metric

or the non-metric discriminant functions were included. Again, we used a stepwise approach to determine which of the combined set of characters contributed most to discrimination of the samples. For this analysis we deleted the three specimens deleted for the metric analysis and the four deleted for the non-metric analysis, leaving a sample of 174.

RESULTS

STATISTICAL TESTS OF DIFFERENCES AMONG THE SAMPLES

The samples from the three areas differed significantly in both metric and non-metric characters. Descriptive statistics for the metric characters are given by area in Table 1. The differences among the groups for the metric characters were large (MANOVA, Wilks' lambda likelihood ratio statistic = 0.0288, $p < 0.0001$). For the non-metric characters, the similarity indices were 0.95 (Black Sea vs. western North Atlantic), 0.97 (western North Atlantic vs. eastern tropical Pacific), and 0.97 (Black Sea vs. eastern tropical Pacific); all these pairwise differences are very significant (chi-square test, $p < 0.001$). For the bootstrap test, the mean number of within-area pairwise differences was 5.51 characters (i.e., two specimens chosen randomly from one area were different in an average of 5.51 out of the 26 non-metric characters). The mean number of between-area pairwise differences was 6.31. The ratio of within- to between-area differences thus was

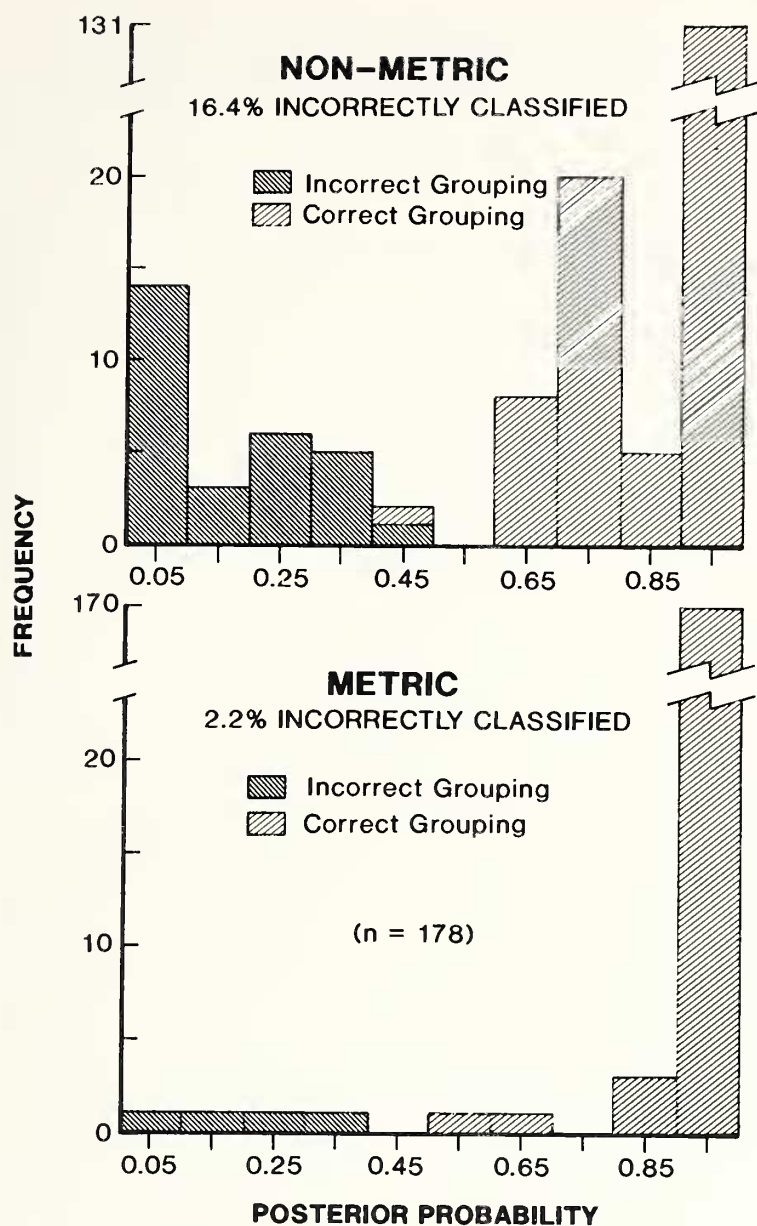


Figure 3. Distribution of posterior probability of correct classification for specimens correctly classified (hatched) and incorrectly classified (shaded), for metric and non-metric discriminant analysis of geographical samples of *Delphinus delphis*.

0.874. A value this small was never observed in 1000 bootstrap samples (hence, $p < 0.001$).

DISCRIMINANT ANALYSES

The metric characters had higher discriminating power than the non-metric characters, but both were efficient. In the metric analyses, 11 characters added to the discrimination of sample origin (Tables 2 and 3). The resulting first and second canonical variables show excellent separation of samples by area of origin (Fig. 2). The jackknife method gives an estimated 97.8% correct classification based solely on these 11 characters (Table 4, Fig. 3). Using non-metric characters, only eight binary variables added to the discrimination of sample origin. These eight corresponded to eight different non-metric characters (Table 5). The first two canonical variables showed good separation of the western North Atlantic sample from the other two but considerable overlap between the Black Sea and

Table 5. Statistics for stepwise discriminant analysis of skulls of *Delphinus delphis* from three areas based on non-metric characters (numbers in parentheses refer to character numbers in Appendix 3), including standardized (by pooled within variances) coefficients for canonical variables.

Step	Binary variable	F-value to enter	Coefficients	
			I	II
1	9 (4)	220.24	-0.31316	0.02323
2	29 (15)	16.72	0.97293	-0.26376
3	31 (16)	8.90	-0.06172	0.19337
4	10 (5)	6.72	0.10358	-0.14793
5	25 (13)	5.07	0.02593	0.18923
6	48 (26)	4.72	0.02346	0.37229
7	18 (9)	4.65	0.00641	0.24421
8	23 (12)	4.32	0.00000	0.00000
Constant:			1.55151	-1.09187

eastern tropical Pacific samples (Fig. 4). This was also reflected in the jackknife classification matrix (Table 4), in which 18 of 31 mis-classifications occurred between these two areas. The average correct classification was 82.5%. The dispersion of posterior probabilities (Fig. 3) was also very much greater than for the metric analysis.

When the 11 metric characters from the metric analysis and the 8 non-metric characters were combined in a third stepwise discriminant analysis, 7 metric and 2 non-metric characters contributed to discrimination of sample origin (Table 6). The jackknife estimate of correct classification was 94.3% (Table 4).

In the first canonical plane, the geographic areas are very distinct (Fig. 5).

DISCUSSION

RELATIVE POWER OF THE TWO TYPES OF CHARACTERS

While both the metric and non-metric characters were effective in discrimination, the two types of characters had different resolving power for different pairs of the three geographical samples. In the combined analysis, a non-metric character was the first variable entered and was very powerful (as indicated by the initial F-value to enter; Table 6) in separating the western North Atlantic sample from the combined Black Sea and eastern tropical Pacific samples, and the additional non-metric variable that entered the analysis also contributed (almost exclusively) to this separation. The seven metric characters that entered the analysis mainly contributed to separation of the Black Sea and eastern tropical Pacific samples. If the non-metric characters are indeed neutral, this may indicate that the western North Atlantic population is relatively the most isolated, with the least genetic exchange with the

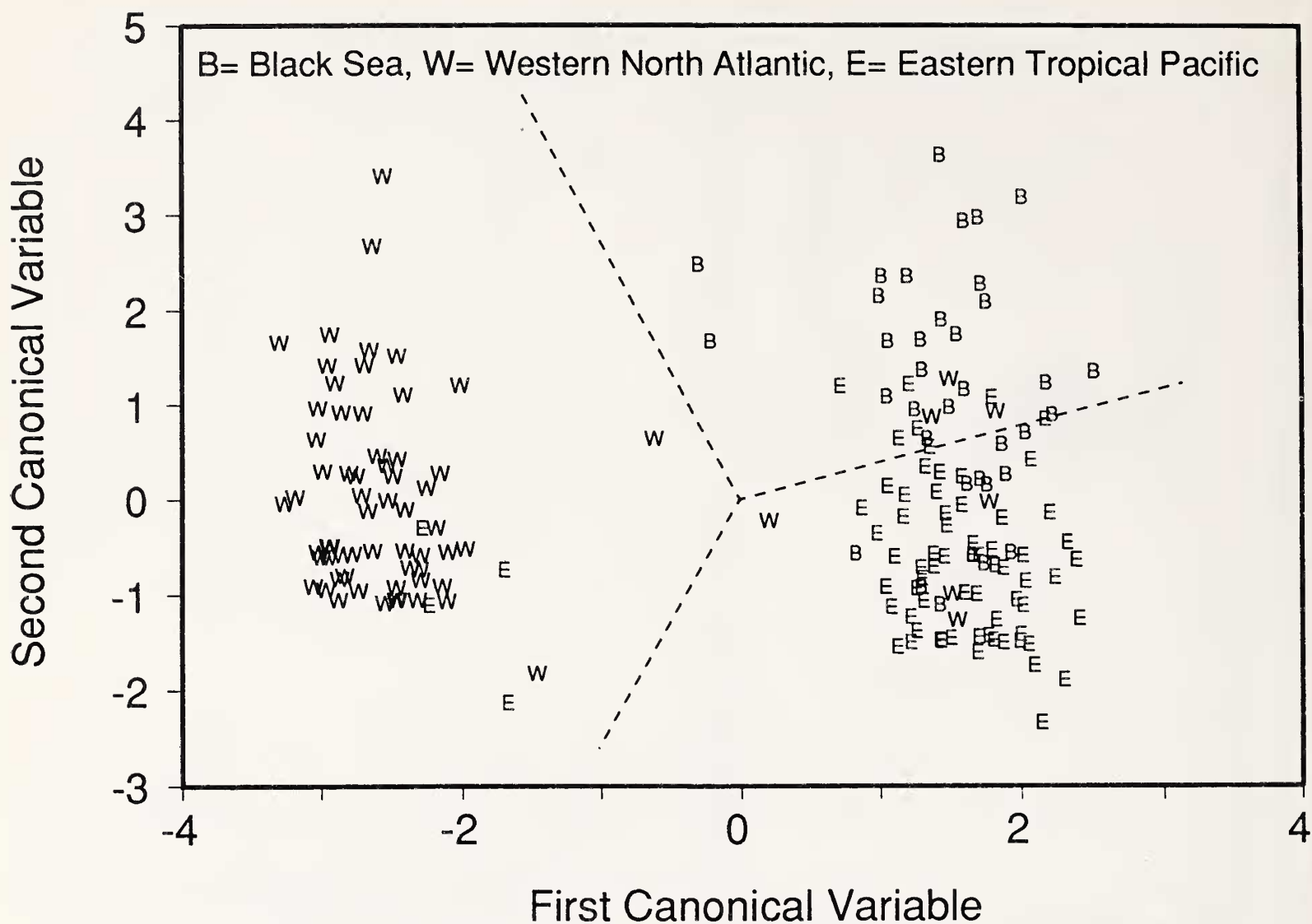


Figure 4. Results of discriminant analysis of geographical samples of skulls of *Delphinus delphis* based on all 26 non-metric characters.

other populations. The converse is that genetic exchange is or has been greatest between the Black Sea and the eastern tropical Pacific. While possible, this seems unlikely. An alternative explanation is that the non-metric characters are not really neutral

Table 6. Statistics for stepwise discriminant analysis of skulls of *Delphinus delphis* from three areas based on combined metric variables and non-metric characters, including standardized (by pooled within variances) coefficients for canonical variables. Non-metric characters listed in Appendix 3; metric acronyms in Appendix 2.

Step	Character	F-value to enter	Coefficients	
			I	II
1	Non-metric 4	233.41	-0.73182	-0.21326
2	ROST	95.55	0.30877	-0.04114
3	BRNH	31.19	0.22978	-0.63139
4	PARI	19.77	0.43258	-0.75298
5	FOSH	31.99	-0.40402	0.05757
6	INTN	15.14	-0.25809	-0.29547
7	TOOW	10.58	-0.34667	0.56602
8	BRNL	9.10	-0.42534	0.22506
9	Non-metric 5	6.57	-0.23313	0.29519
		Constant:	19.54346	26.24044

or are somehow linked chromosomally to metric characters directly subject to selection pressure (i.e., the results for both character sets reflect primarily differential selection pressures rather than genetic isolation) and that the closer morphological distance between the Black Sea and eastern tropical Pacific samples in both character suites represents adaptive convergence. If this is the case, then the metric characters must be considered to be relatively more useful, as their use resulted in fewer errors of classification.

The differential power to resolve various pairs of geographical samples could also relate to the fact that the western North Atlantic sample was drawn from a much larger area and was more heterogeneous than the other two samples, in both metric (Fig. 6) and non-metric (Fig. 4) characters.

These questions could usefully be addressed by a comparison of metric and non-metric differences between two parapatric populations that are differentiated morphologically but between which some gene flow occurs (as evidenced by intergradation or hybridization). Ideally, this would be coupled with a parallel analysis of DNA (e.g., sequencing or restriction-enzyme analysis of highly variable regions of the mitochondrial DNA molecule) to estimate relative gene flow between the popula-

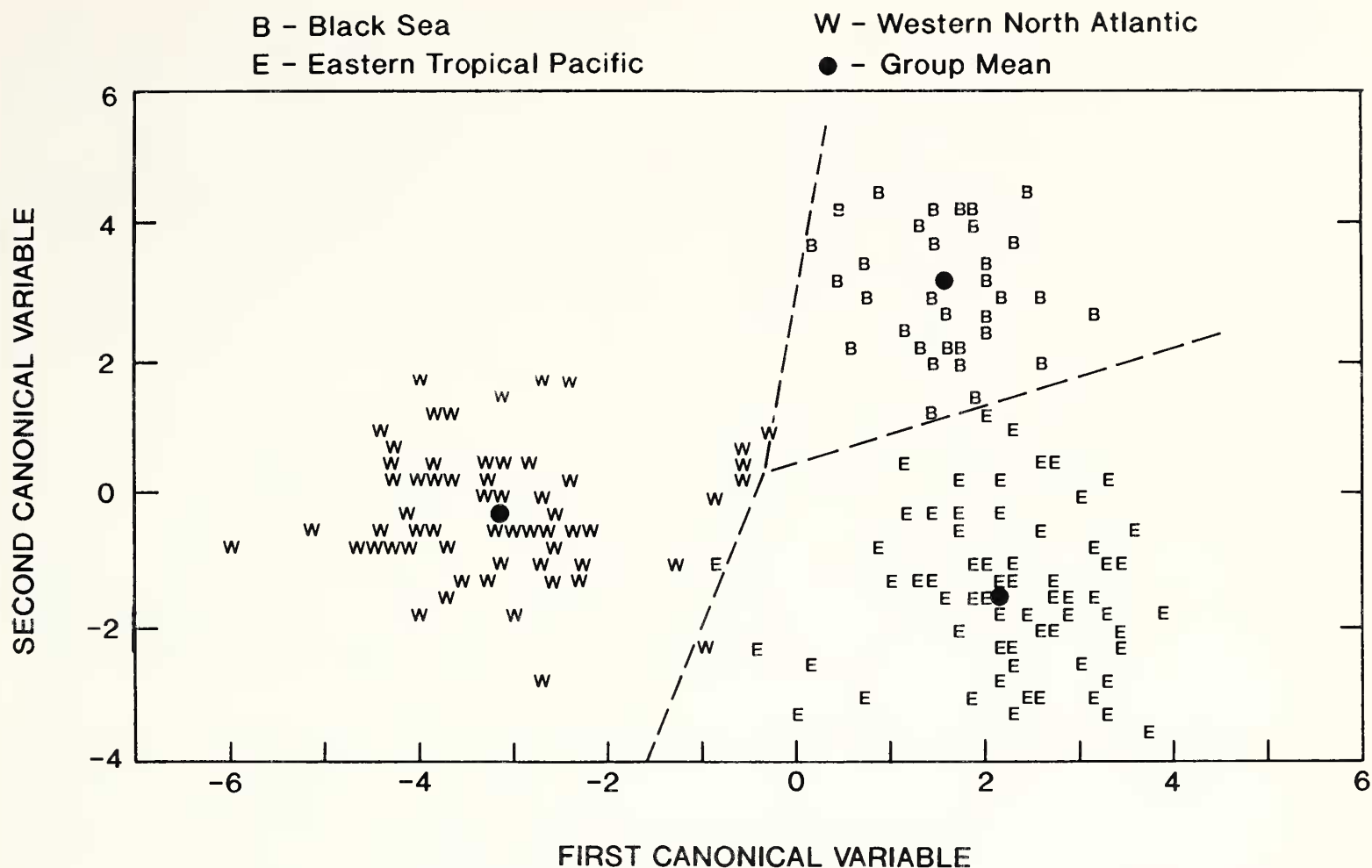


Figure 5. Results of discriminant analysis of geographical samples of skulls of *Delphinus delphis* based on combined metric and non-metric characters.

tions. The question of the relative coherence of the Atlantic sample should be addressed by analyses of samples from more limited areas as they become available.

REPEATABILITY

The two scorers had considerable difficulty in maintaining repeatability in scoring the non-metric characters. Despite the character states ostensibly being objectively defined, there proved to be some difficulty and subjectivity in consistently discriminating between them for some skulls, because of subtle variation among individual skulls in size, shape, and placement of the features, and the scorers found that there was a constant need to cross-check and consult with each other to prevent character drift over a period of even a few days. We believe that there is a definite possibility that significant drift may have occurred between the Moscow and Washington, D.C., sessions. To address this problem, ideally all specimens to be included in a non-metric study should be physically pooled and scored in random order in a short period of time in one location. The comparability of data collected by different investigators or by one investigator at widely separated times must be questioned.

Of course, poor comparability of data collected by different workers is not a problem only of non-metric characters; even meristic characters can show

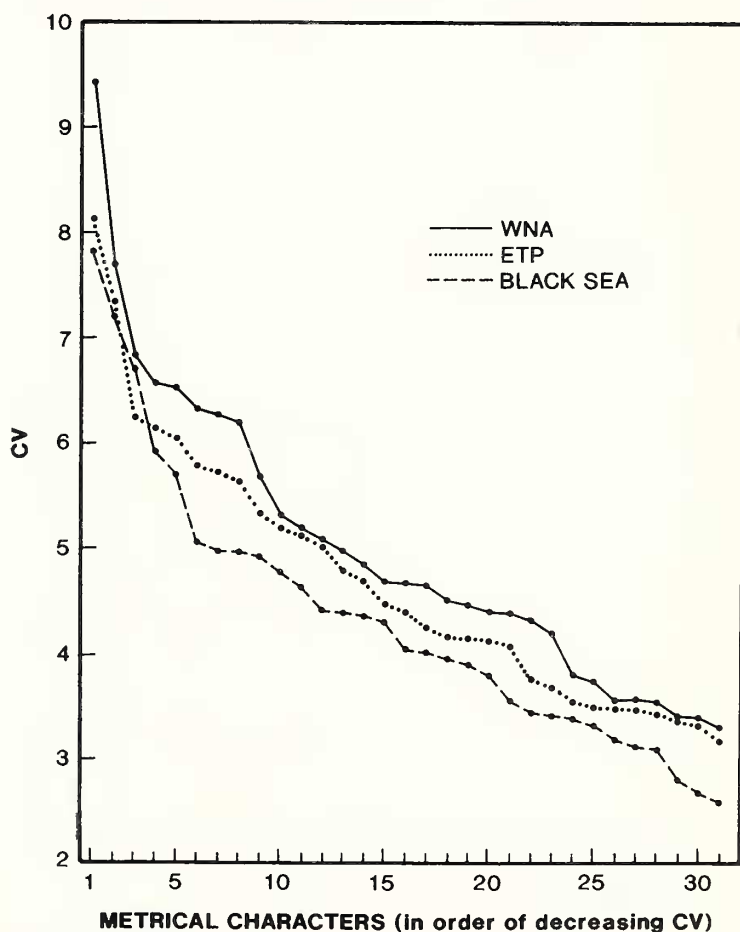


Figure 6. Coefficients of variation (CV) for 31 cranial characters for three geographical samples of *Delphinus delphis*. The characters on the horizontal axis are in order of decreasing CV; the order differs among the three series. The areas under the curves are proportional to the total relative variation for the characters.

such variation (Perrin et al., 1987). Of special concern here, however, is possible drift for single workers over a relatively short period of time.

Because of their apparent lesser resolving power and because of the difficulties concerning repeatability, we recommend that non-metric characters be used in dolphin population studies only in combination with metric characters. If non-metric characters are used, special attention should be paid to controlling conditions to maximize comparability of data sets.

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LITERATURE CITED

Berry, R.J. 1969. Non-metric skull variation in two Scottish colonies of the Gray seal. *Journal of Zoology (London)* 157:11-18.

Dailey, M.D., and W.F. Perrin. 1973. Helminth parasites of porpoises of the genus *Stenella* in the eastern tropical Pacific, with descriptions of two new species: *Mastigonema stenellae* gen. et sp. n. (Nematoda: Spiruroidea) and *Zalophotrema pacificum* sp. n. (Trematoda: Digenea). *Fishery Bulletin, U.S.* 71: 455-471.

Dixon, W.J., M.B. Brown, L. Engelman, and R.I. Jennrich (eds.). 1990. *BMDP statistical software manual*. Two vol. Berkeley, Calif.: Univ. Calif. Press, 1386 pp.

Fedoseev, G.A. 1984. Use of nonmetrical characters of skulls of Bering Sea seals in a study of the phenotypic structure of their populations. In *Soviet-American cooperative research on marine mammals. Volume 1—Pinnipeds*, ed. F.H. Fay and G.A. Fedoseev. NOAA Technical Report NMFS 12, 99 pp.

Hartman, S.E. 1980. Geographic variation analysis of *Dipodomys ordii* using nonmetric cranial traits. *Journal of Mammalogy* 61:436-448.

Kinze, C.C. 1985. Intraspecific variation in Baltic and North Sea harbour porpoises (*Phocoena phocoena* (L., 1758)). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 146:63-74.

Kinze, C.C. 1990. *Non-metric analysis of harbour porpoises (Phocoena phocoena) from the North and Baltic Seas: Implications for stock identity*. International Whaling Commission meeting document SC/42/SM35, 23 pp. (available from IWC).

Perrin, W.F. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography* 21:1-206.

Perrin, W.F., E.D. Mitchell, J.G. Mead, D.K. Caldwell, M.C. Caldwell, P.J.H. van Bree, and W.H. Dawbin. 1987. Revision of the spotted dolphins, *Stenella* spp. *Marine Mammal Science* 3:99-170.

Perrin, W.F., M.D. Scott, G.J. Walker, and V.L. Cass. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Technical Report NMFS 28, 28 pp.

Perrin, W.F., A.V. Yablokov, and V.L. Cass. 1982. Preliminary report on the use of non-metrical skull characters to discriminate populations of pelagic dolphins. *Southwest Fisheries Center Administrative Report* LJ-82-14, 32 pp.

Perrin, W.F., A.V. Yablokov, J. Barlow, and M.V. Mina. 1988. The use of non-metrical skull characters for analyzing geographical variation in the common dolphin, *Delphinus delphis*. Part I: Selection of characters. *Southwest Fisheries Center Administrative Report* LJ-88-20, 24 pp.

Sjøvold, T. 1973. The occurrence of minor non-metrical variants in the skeleton and their quantitative treatment for population comparisons. *Homo* 24:204-233.

Tomilin, A.G. 1957. Kitoobraznye [Cetaceans], vol. 9. In *Zveri SSSR i prilezhanshchikh stran. Zveri vos-tochnoi Evropy i severnoi Azii [Mammals of the U.S.S.R. and adjacent countries. Mammals of eastern Europe and northern Asia]*, ed. V.G. Heptner. Moscow: Akad. Nauk SSSR, 756 pp. (Transl. by O. Ronen, Cetaceans. In *Mammals of the U.S.S.R. and adjacent countries. Mammals of eastern Europe and adjacent countries [sic]*. Israel Program for Scientific Translations, Jerusalem, 1967, 717 pp.)

Urbach, V.Y. 1964. *Biometric methods* [in Russian]. Moscow: Nauka, 416 pp.

Yablokov, A.V., W.F. Perrin, and M.V. Mina. 1983. Otsenka feneticheskikh otnosheniy gruppirovok del'finov na osnove analiza nemetricheskikh variatsiy cherepa [Evaluation of phenetic relations among groups of dolphins using analysis of non-metrical cranial variation]. *Zoologicheskii Zhurnal* 62:1887-1896.

Zhivotovskiy, L.A. 1982. Pokazateli populyatsionnoy izmenchivosti po polimorfnykh priznakam [Indices of population variation in polymorphic characters]. In *Fenetika populyatsiy*, ed. A.V. Yablokov, 38-44. Moscow: Nauka.

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APPENDIX 1

Specimens used in analyses of geographical samples of *Delphinus delphis* are listed below. Black Sea specimens are in the collection of the Zoological Museum, Moscow State University, Moscow (MSUZM); eastern tropical Pacific and western North Atlantic specimens are in the U.S.

BLACK SEA

Batumi, 4 (MSUZM S-5411, S-80352-53, 62); Yalta, 13 (MSUZM S-50804-05, S-80335-36, S-80339-40, S-80363, S-80372-73, S-80376, S-80379, S-80534); Novorossiysk, 14 (MSUZM S-80334, 345, 349, 355, 359, 367, 369, 374-75, 378, 383, 385); unknown localities on the Soviet coast of the Black Sea, 6 (MSUZM S-80342, 347, 360, 377, 387, 389).

EASTERN TROPICAL PACIFIC

9°N, 84°10'W, 14 (USNM 487766-67, 69-70, 73-82); 8°25'N, 84°W, 19 (USNM 487807, 09-12, 15, 17-26, 28-30); 9°18'N, 84°46'W, 1 (USNM 487480); 8°08'N, 87°54'W, 5 (USNM 5000060-61, 65-66); 7°32'N, 83°54'W, 18 (USNM 5000069-80, 82-85, 87-88); 7°25'N, 84°02'W, 1 (USNM 500092); 8°14'N, 83°15'W, 1 (USNM 500116); 7°45'N, 90°50'W, 12 (USNM 500315-16, 20-23, 34-39); 8°40'N, 84°32'W, 2 (USNM 500340-41).

WESTERN NORTH ATLANTIC

Nova Scotia, 2 (USNM 300191-92); 43°32'N, 64°25'W, 1 (USNM 267968); 42°58'N, 63°43'W, 1 (USNM 267969); 40°11'N, 73°33'W, 2 (USNM 571202-03); 39°39'N, 71°54'W, 1 (USNM 20873); 39°20'N, 72°44'W, 7 (USNM 550808-15); 39°N, 73°35'W, 1 (USNM 550781); 38°48'N, 73°05'W, 1 (USNM 550779); 38°54'N, 73°01'W, 1 (USNM 550870); 38°56'N, 72°53'W, 1 (USNM 550750); 38°38'N, 73° 14'W, 2 (USNM 550774-75); 38°38'N, 73°14'W, 1 (USNM 550775); 38°35'N, 73°17'W, 1 (USNM 550550); 38°14'N, 73°44'W, 1 (USNM 550862); 38°11'N, 73°46'W, 1 (USNM 550780); 37°57'N, 74°39'W, 1 (USNM 550927); 37°47'N, 74°52'W, 1 (USNM 550776); 37°44'N, 74°44'W, 1 (USNM 550987); 37°27'N, 74°28'W, 1 (USNM 504654); 37°18'N, 75°01'W, 1 (USNM 550885); Massachusetts, 19 (USNM 21525-5, 5500041, 192, 201, 205-07, 211, 450, 470, 4756, 478, 841, 846-47, 849, 571232); New York, 5 (USNM 7063, 504262-63, 504421, 550755); New Jersey, 1 (USNM 504407); North Carolina, 8 (USNM 4115, 21917-8, 305126, 504219, 504406, 504877-78); Virginia, 7 (USNM 22528, 22560, 395923, 504323, 504958, 550065, 550819); Florida, 1 (USNM 267478); 46°55'N, 27°51'W, 1 (USNM 504631).

APPENDIX 2

Metric skull characters used in the analysis of samples of *Delphinus delphis* from three areas, with acronyms used in tables, are listed below. Measurements are illustrated in Perrin (1975). Tooth width (no. 31) was measured in millimeters and tenths; all others in millimeters.

Character	Acronym
1. Condylobasal length	CBLN
2. Length of rostrum	ROST
3. Rostrum width at base	ROSW
4. Rostrum width at quarter-length	ROSQ
5. Rostrum width at half-length	ROSH
6. Rostrum width at three-quarters-length	ROS3
7. Width of premaxillaries at half-length	PMXH
8. Tip of rostrum to external nares	TIPN
9. Tip of rostrum to internal nares	TIPP

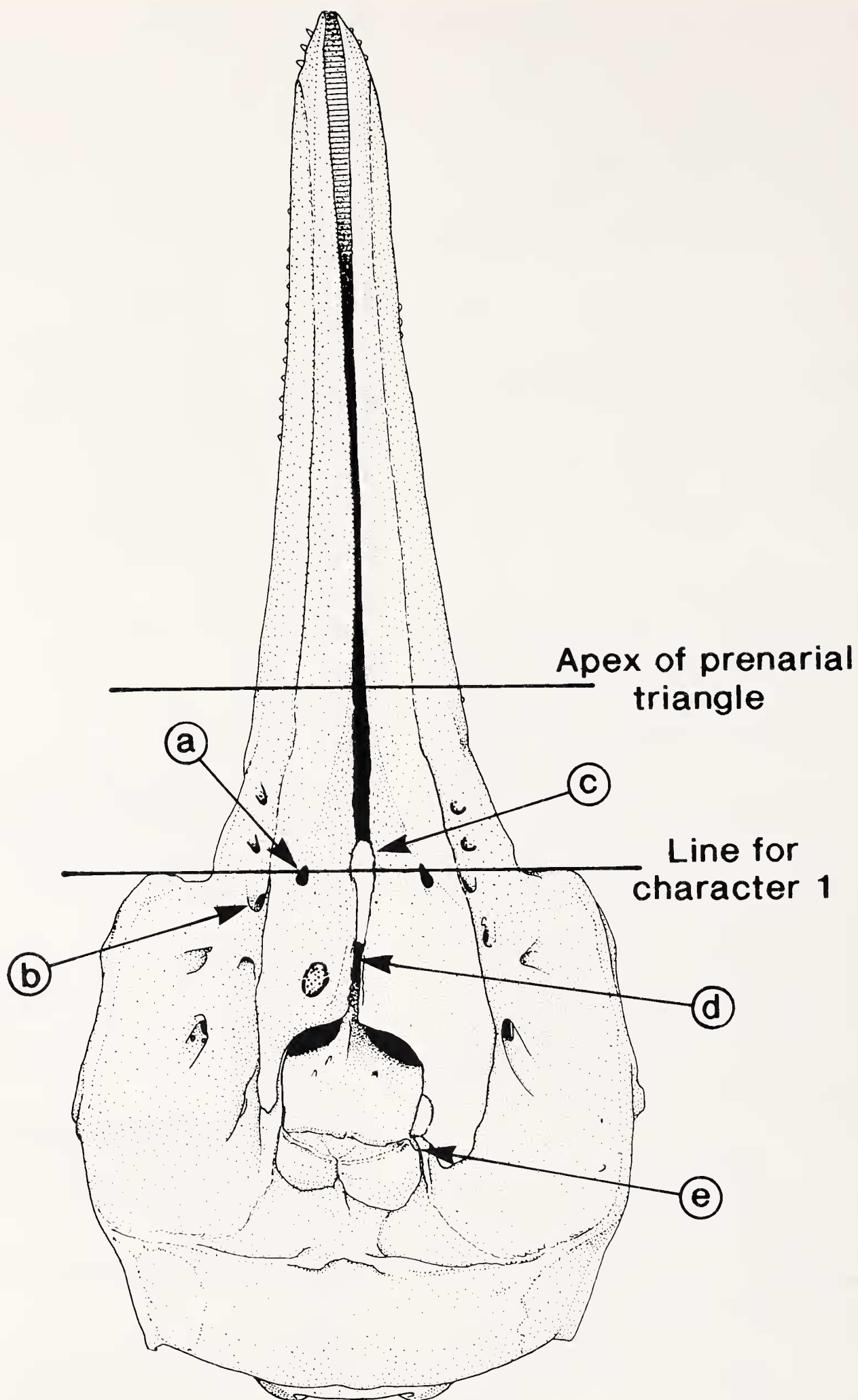
Character	Acronym
10. Preorbital width	PREO
11. Postorbital width	POST
12. Zygomatic width	ZYGO
13. Width of external nares	EXTN
14. Maximum width across premaxillaries	PMXM
15. Parietal width	PARI
16. Braincase height	BRNH
17. Braincase length	BRNL
18. Length of temporal fossa	FOSL
19. Height of temporal fossa	FOSH
20. Length of orbit	ORBI
21. Length of antorbital process	ANTO
22. Width of internal nares	INTN
23. Length of upper toothrow	UPRO
24. Number of upper left teeth	UPTL
25. Number of upper right teeth	UPTR
26. Number of lower left teeth	LOTL
27. Number of lower right teeth	LOTR
28. Length of lower toothrow	LORO
29. Length of ramus	RAML
30. Height of ramus	RAMH
31. Width of tooth at alveolus	TOOW

APPENDIX 3

Non-metric cranial characters used in the analysis of geographical samples of *Delphinus delphis* are as follows.

IN DORSAL VIEW

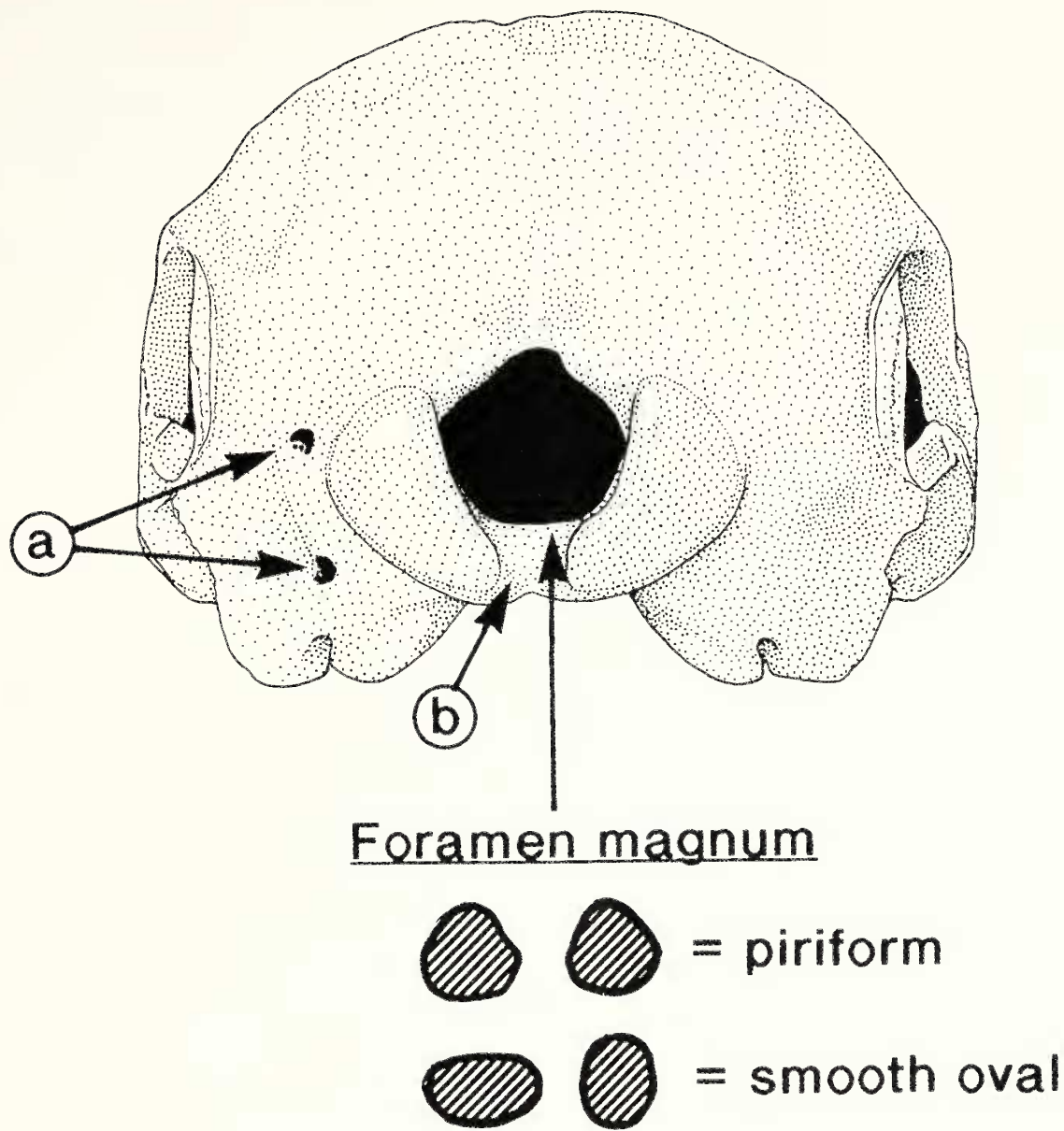
1. Position of anterior edge of mesial infraorbital foramen (a in App. Fig. 1) relative to the level of the anteriormost projection of the antorbital process, on left side. Note: The level of the antorbital process must be determined accurately; this is best done with a flexible ruler or other straight-edge.
Codes: 1 = ahead, 2 = behind, 3 = at level, or uncertain.
2. Position of posterior edge of lateral infraorbital foramen (first, if more than one on each side) (b in App. Fig. 1) relative to posterior edge of mesial infraorbital foramen (a in App. Fig. 1), on left side.
Codes: 1 = ahead, 2 = behind, 3 = at the level, or uncertain.
3. Number of vertical perforations (visible in vertical view) of facial area of maxillary by foramina, on right side.
Codes: 1 = 1, 2 = 2, . . . , 9 = 0.
4. Dorsal projection of mesethmoid between premaxillaries near base of rostrum (c in App. Fig. 1).
Codes: 1 = below surface of premaxillaries, 2 = above surface, 3 = at surface, or uncertain.
5. Contact or near-contact (<1-mm gap) between premaxillaries (or exposed maxillaries) in prenarial triangle (c in App. Fig. 1). Caution: The skull must be rotated to allow detection of overlapping bones.
Codes: 1 = present, 2 = absent, 3 = uncertain.
6. Contact between premaxillary and nasal (no intervening bones), on left side (e in App. Fig. 1).
Codes: 1 = present, 2 = absent, 3 = uncertain.



Appendix Figure 1. Dorsal view of dolphin skull, showing features mentioned in descriptions of non-metric characters.

7. Same on right side.
 8. Relative extension of ascending process of left premaxillary. Note: Do not confuse with anterior extension of nasal between premaxillary and maxillary.

Codes: 1 = beyond (posterior to) anterior edge of left nasal, 2 = not beyond (anterior to) anterior edge of left nasal, 3 = at the level of anterior edge of left nasal or uncertain.



Appendix Figure 2. Occipital view of dolphin skull, showing features mentioned in descriptions of non-metric characters.

IN OCCIPITAL VIEW (Resting Right-Side-Up on Table)

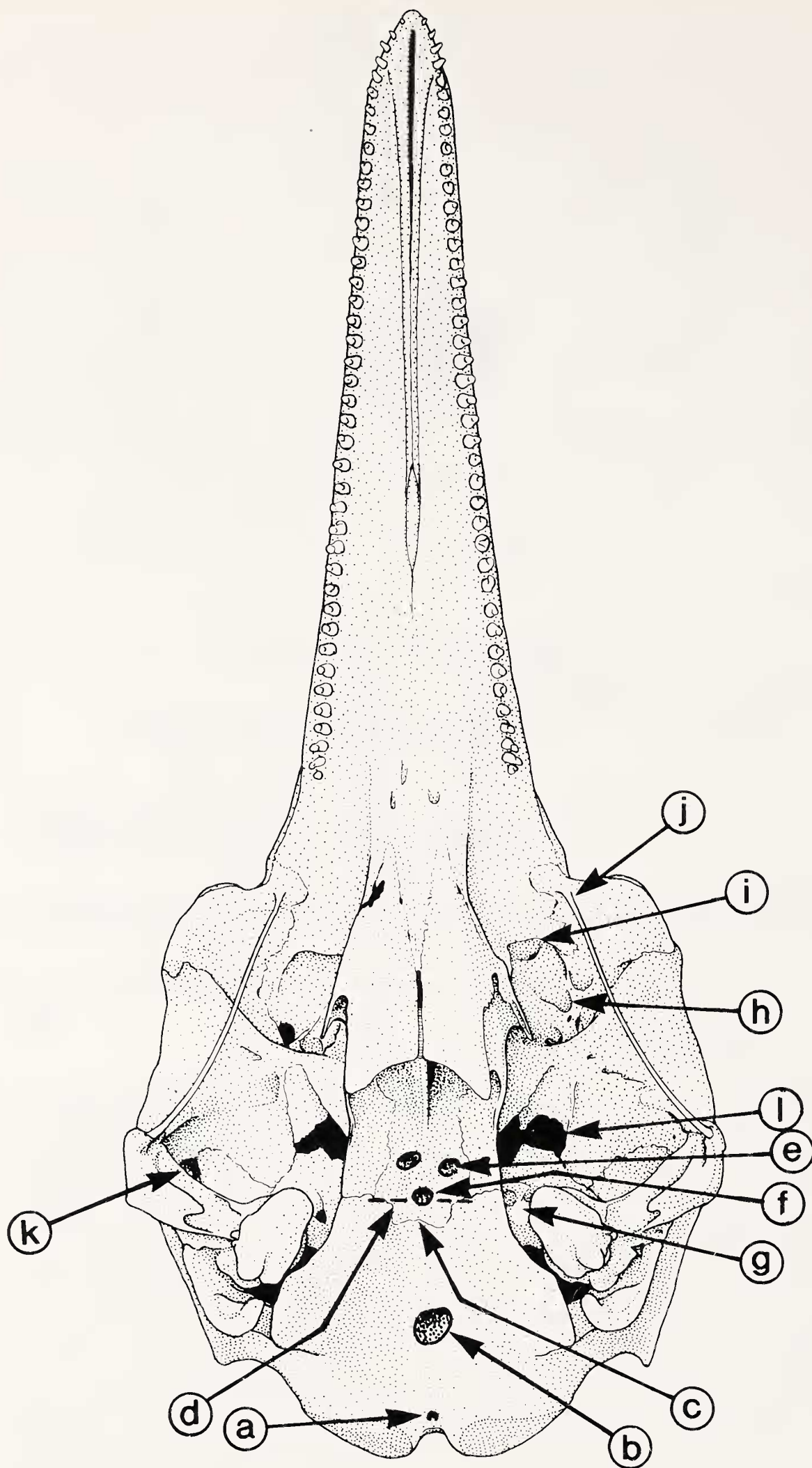
9. Shape of foramen magnum (App. Fig. 2).
Codes: 1 = piriform, 2 = smooth oval/circle, 3 = uncertain.
10. Number of fenestrations in occipital (near foramen magnum) and exoccipital (a in App. Fig. 2), on left side.
Codes: 1 = 1, 2 = 2, 3 = 3, ..., 9 = 0.
11. Same on right side.
12. Groove between occipital condyles, in occipital profile (b in App. Fig. 2).
Codes: 1 = clearly present, 2 = clearly absent, 3 = absent, or uncertain.

IN VENTRAL VIEW

13. Small foramen between occipital condyles in basoccipital (a in App. Fig. 3).
Codes: 1 = present, 2 = absent, 3 = uncertain.
14. Mesial fenestrations in basoccipital (b in App. Fig. 3).
Codes: 1 = present and clearly natural, 2 = absent,

- or clearly postmortem damage, 3 = present, but possibly postmortem damage (= uncertain).
15. Position of posterior end of vomer^a (c in App. Fig. 3) relative to line connecting mesial ends of sutures between alisphenoids and exoccipitals (d in App. Fig. 3).
Codes: 1 = behind (ignoring small irregularities), 2 = in line or ahead, 3 = uncertain.
16. Lateral fenestration in vomer^a (e in App. Fig. 3), on left side.
Codes: 1 = present, 2 = absent, 3 = uncertain.
17. Same on right side.
18. Mesial fenestration in vomer^a (f in App. Fig. 3).
Codes: 1 = present, 2 = absent, 3 = uncertain.
19. One or more fossae between the mesial and posterior lacerate foramina (g in App. Fig. 3), on left side.
Codes: 1 = present, 2 = absent, 3 = uncertain.
20. Position of interior opening of supraorbital foramen (h in App. Fig. 3), on left side.
Codes: 1 = behind (under) frontal trabeculum (hid-

a. Erroneously called basisphenoid in Yablokov et al. (1983) and Perrin et al. (1982, 1988).



Appendix Figure 3. Ventral view of dolphin skull, showing features mentioned in descriptions of non-metric characters.

den in perpendicular view), 2 = anterior to frontal trabeculum (visible), 3 = at trabeculum, or uncertain.

21. Position of anterior edge of large ventral foramen in maxillary (i in App. Fig. 3) relative to posterior edge of base of jugal (j in App. Fig. 3), on left side.

Codes: 1 = anterior to edge of jugal, 2 = posterior to edge, 3 = at edge, or uncertain.

22. Same on right side.

23. Foramen-like fossa in internal roof of temporal fossa (k in App. Fig. 3; shown on right side), on left side.

Codes: 1 = present, 2 = absent, 3 = uncertain.

24. Same on right side.

25. Configuration of optical hiatus (l in App. Fig. 3), on left side.

Codes: 1 = perforated in vertical view (>1-mm opening), 2 = not perforated, 3 = uncertain.

26. Same on right side.